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Hays, G., Mortimer, J., Ierodiaconou, D. & Esteban, N. (2014). Use of Long-Distance Migration Patterns of an Endangered Species to Inform Conservation Planning for the World's Largest Marine Protected Area. *Conservation Biology*, 28(6), 1636-1644.
<http://dx.doi.org/10.1111/cobi.12325>

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**Use of long-distance migration patterns of an endangered species to inform
conservation planning for the world's largest marine protected areas**

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Version accepted by Conservation Biology on 26 February 2014

Short title: Turtle migration from Chagos Archipelago

Key words: Argos, GPS tracking, *Chelonia*, Chagos, MPA, reserve

Word count: 5600

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Abstract

Large marine protected areas (MPAs), each hundreds of thousands of square kilometers, have been set up by governments around the world over the last decade as part of efforts to reduce ocean biodiversity declines, yet their efficacy is hotly debated. The Chagos Archipelago MPA (640,000 km²) (Indian Ocean) lies at the heart of this debate. We conducted the first satellite tracking of a migratory species within the MPA, the green turtle (*Chelonia mydas*), and assessed the species' use of protected versus unprotected areas. We developed an approach to estimate length of residence within the MPA that may have utility across migratory taxa including tuna and sharks. We recorded the longest ever published migration for an adult cheloniid turtle (3979 km). Seven of 8 tracked individuals migrated to distant foraging grounds, often > 1000 km outside the MPA. One turtle traveled to foraging grounds within the MPA. Thus, networks of small MPAs, developed synergistically with larger MPAs, may increase the amount of time migrating species spend within protected areas. The MPA will protect turtles during the breeding season and will protect some turtles on their foraging grounds within the MPA and others during the first part of their long-distance post-breeding oceanic migrations. . International cooperation will be needed to develop the network of small MPAs needed to supplement the Chagos Archipelago MPA.

Introduction

Marine protected areas (MPAs) range from networks of small targeted coastal MPAs (e.g. Jones 2012) up to vast MPAs ($>100,000 \text{ km}^2$) that cover both coastal and pelagic areas (Scott et al. 2012; Pala 2013*a,b*). However there is growing awareness that across this size spectrum the effectiveness of MPAs needs to be established to allow informed decisions to optimize biodiversity preservation (Halpern & Warner 2003; Game et al. 2009; Agardy et al. 2011). For example, after the US designation in 2006 of $362,000 \text{ km}^2$ around the Hawaiian Islands as a protected area, the UK Government followed suit in 2010 by creating an even bigger MPA ($640,000 \text{ km}^2$) around the Chagos Archipelago in the Indian Ocean, making it the world's largest MPA at the time (Sheppard et al. 2012). This trend toward establishing large MPAs continues (Cressey 2011; Pala 2013*a*). The Chagos MPA encompasses some of the most pristine coral reefs in the ocean and hosts a number of endangered species (Sheppard et al. 2012). Yet there has been heated debate as to whether even these largest MPAs, such as the Chagos Archipelago, are large enough to provide effective protection for migratory species, prompting the call for tracking studies to be undertaken (Pala 2013*a,b*). We conducted the first satellite tracking of a migratory species within the MPA and assessed the species' use of protected versus unprotected areas. Migratory taxa may exhibit different types of long distance movements. For example, turtles often shuttle between small breeding and foraging areas, whereas fish may range more broadly. We set out to show how empirical data on movement can be used to assess key areas for protection for migratory species. While our work focusses on sea turtles, we believe the general method may have broad applicability for other migratory taxa, including endangered (e.g., some sharks) and commercially exploited groups (e.g., tuna).

One of the high profile endangered migratory species within the Chagos Archipelago is the green turtle (*Chelonia mydas*), which nests widely on the atolls in the area (Mortimer & Day 1999). Elsewhere in the world green turtles, and other species of sea turtles, migrate long distances from their breeding areas to their foraging grounds (e.g., reviewed in Hays and Scott [2013]). However, long distance migration in post-breeding sea turtles is not ubiquitous. For example, satellite tracking shows that some adult green turtles on the Cocos Keeling Islands (eastern Indian Ocean) are non-migratory (Whiting et al. 2008). Given the international interest in the Chagos MPA, we satellite tracked green turtles breeding within the MPA. We calculated the extent of their movements and considered the implications of these movements for conservation planning and the wider applicability of our findings for the conservation of other migratory groups (such as tuna) within the context of large MPAs.

Methods

Satellite tracking

All work was approved by Swansea University Ethics Committee and the BIOT Scientific Advisory Group (SAG) of the UK Foreign and Commonwealth Office. Satellite tags were attached to nesting green turtles on the island of Diego Garcia (7°25'S, 72°27'E) within the Chagos Archipelago during October 2012. Turtles were located while they were nesting ashore at night. Once turtles were returning to the sea they were restrained in a large open topped and bottomless wooden box. The carapace was first cleaned with acetone and then lightly sandpapered to provide a better surface for attachment of the tag. Satellite tags were then attached with quick setting epoxy (Pure-2K, Powerfasteners Inc., New Rochelle, NY, USA). We smoothed the epoxy to provide a streamlined shape and then covered the epoxy and transmitters with anti-fouling paint (Trilux 33, International, www.yachtpaint.com). Size

of tagged turtles and tracking details are in Table 1. The attachment process took around 2 h to complete, after which the turtle was allowed to return to the sea.

We used 2 models of satellite tags (model F4G 291A, Sirtrack, Havelock North, New Zealand, and SPLASH10-BF, Wildlife Computers, Seattle, USA), both of which relayed Fastloc-GPS data via the Argos satellite system (<http://www.argos-system.org/>). Satellite tags were programmed to acquire a maximum of one Fastloc-GPS location every 15 minutes. However, in reality fewer Fastloc-GPS locations were obtained, presumably because of the intermittent surfacing of the turtles. Only Fastloc-GPS positions obtained with a minimum of 4 satellites and with a residual error value of <35 were used. These locations were generally within a few to tens of metres of the true location. We designated the start of the post-nesting migration as the time at which individuals left Diego Garcia and began their oceanic crossing, which continued (i.e., there was no return to the nesting beaches) until they arrived at the foraging grounds. A small number ($<0.05\%$) of locations were removed because they looked visibly erroneous when the tracks were viewed in Google Earth (i.e., they were off the path of previous and subsequent locations). An analysis of the speed of travel always confirmed these locations necessitated unrealistic speeds of travel (>200 km/day). We considered areas where turtles slowed down and stayed to be foraging sites. These foraging sites were always shallow coastal areas, and we obtained location data from these residence sites for a minimum of 2 months before transmissions ceased. In some cases tags were still functioning after an individual had been on its foraging grounds for >1 year and showed no further movement to other foraging sites. As of January 2014, some tags were still functioning, 15 months after attachment. We analyzed data collected up to 1 August 2013.

Delineating foraging areas and space use at breeding grounds

Kernel density estimations (KDE), a technique for objectively assessing space use, were calculated using the Geospatial Modelling Environment (GME) version 7.2.1 extension for ARCGIS (version 10.1, ESRI, Redlands, California). Cell size was 30 m, and we used least-squares cross validation (LSCV) to determine bandwidth (Beyer 2012; R Core Development Team 2013). Estimates of area use were calculated for each foraging individual and combined across individuals to determine space use during residence at the breeding grounds at Diego Garcia. Volume of the KDE distributions was used to derive contours representing 50%, 90%, and 95% estimates of area use. We used the global topography data source SRTM30 PLUS version 8 to estimate foraging grounds for the entire Amirantes Islands group (Becker et al. 2009). We used the SRTM data to extract area estimates for depths of <50 m as a proxy for the extent of foraging habitat.

Life history model for time allocation

We used literature values to parameterize a life history model to estimate green turtle time of residence in the Chagos Archipelago MPA. Key components of the migration cycle of adult female sea turtles are the remigration interval, i.e. the length of time between breeding seasons; arrival at the breeding area for a mating season; and the laying of several clutches of eggs during each breeding season. The remigration interval and clutch frequency of sea turtles have been assessed at rookeries around the world by attaching numbered flipper tags to individuals so they can be identified when they come ashore to nest. For example, tagging data for green turtles from Aldabra (Indian Ocean) suggest a typical remigration interval of at least 3-5 years (Mortimer et al. 2011). Observations of mating pairs and the subsequent nesting of females suggest that female green turtles may arrive at the breeding ground at least 1 month prior to the start of nesting (Godley et al. 2002). Typically green turtles are thought to lay at least 3 clutches in a season (Mortimer & Carr 1987), which may be an underestimate

because some clutches are unobserved (Weber et al. 2013). We used these best estimates of breeding periodicity.

Results

Space use at the breeding grounds and post-nesting migrations

We obtained Fastloc-GPS location data for all individuals for several months and typically we obtained several locations each day (Table 1). After satellite tag attachment some individuals migrated away from Diego Garcia within a few days, while others remained at the island for several weeks. During their residence at Diego Garcia, the turtles tended to be close (within a few kilometers) to the nesting beach before individuals traveled along the west coast and departed from the island in a westerly to northwesterly direction en route to their foraging areas (Figure 1).

Four individuals traveled more than 2500 km westwards from the Chagos Archipelago to the Amirantes Islands (Seychelles); two turtles traveled >3800 km westwards to the coast of Somalia on mainland Africa; one turtle traveled >1000 km northwards to the Maldives (Figure 2). Only one of the 8 tracked turtles remained in the Chagos Archipelago MPA; it traveled 166 km to foraging grounds on the Great Chagos Bank, which lies north of the original nesting beach.

Model of time allocation within the MPA

The model showed that when a female turtle arrived at the breeding grounds 30 d before producing its first clutch and then laid 3 further clutches at 15-d intervals before departing from the breeding grounds, it was resident at the breeding grounds for a total 75 d. During migration the turtles traveled approximately 500 km from the nesting beach before reaching the boundary of the MPA, which at a speed of 60 km/d (Table 1) took around 8 days to

complete. When individual females bred every 3 years, over a 3-year (1095-d) breeding cycle a turtle spent 91 d (8.3% of the time) in the MPA (75 d at the nesting beaches and 16 d traveling to and from the nesting beaches within the MPA). That adult female turtles spent most of their time outside the MPA was relatively insensitive to the exact parameterisation of the life-history model in terms of breeding periodicity and length of time in residence in the nesting areas (Figure 3). When the remigration interval was 5 years for turtles nesting at the Chagos MPA, then repeating the calculations above produced an estimate of 5.0% for the time spent within the MPA. Since our findings for time allocation between breeding and foraging areas were relatively insensitive to the exact values used in the model, our key conclusions are robust.

Space use on foraging grounds and habitat mapping

The foraging grounds of individuals were always shallow coastal sites regardless of whether individuals traveled to a mainland coast or an island (Figure 4 and 5). On the foraging grounds, generally several 100 locations were obtained per individual (Table 1). The turtle that traveled to the Chagos Bank stayed within the Chagos MPA. However, the 7 other turtles traveled to foraging grounds that were not within MPAs. Generally, on the foraging grounds individuals were located in water shallower than 50 m. Such depths had limited areal extent (Figure 4 and 5). For example, in the Amirantes Islands (Seychelles) the total area shallower than 50 m was estimated as 3,254 km² (Figure 5), which is only 0.5% of the size of the existing Chagos MPA.

Discussion

Our results highlight the value of large MPAs for a migratory species and how conservation planning could be further enhanced based on empirical tracking data. We believe our

methods have value for other migratory taxa such as tuna, whose use of MPAs has been the topic of heated debate (Pala 2013*a,b*).

The Chagos MPA has great value for protecting a range of habitats such as the coral reefs and their associated fauna and flora (Sheppard et al. 2012). Our findings emphasize the value of the full protection sea turtles currently receive within the Chagos MPA. Our tracking results show how the Chagos MPA protects adult green turtles during the breeding season because they remain within the MPA close to their nesting beaches. Similarly limited movements within the breeding season have been reported for some other sea turtle populations (Schofield et al. 2013*a*). Furthermore, the few adults that travel to foraging grounds within the MPA will remain in protected areas outside the breeding season. In addition, the protection of nests located on beaches in the heart of the MPA will help increase hatchling success (i.e., the proportion of eggs laid that result in hatchlings successfully emerging from nests).

The protection of nesting beaches within the Chagos archipelago is particularly important because sea turtle conservation programs elsewhere have shown how increasing hatchling success and protecting breeding adults can drive long-term increases in population size (Balazs & Chaloupka 2004; Dutton et al. 2005; Nel et al. 2013). Several sea turtle populations nesting at protected sites in the Indian Ocean are increasing or stable (Lauret-Stepler et al. 2007, Bourjea et al. 2007, Mortimer et al. 2011), despite relatively high rates of mortality on feeding grounds along the coastlines of east Africa and Madagascar (Hughes 1982; Mortimer 2001, Humber et al. 2011).

The current conservation value of the Chagos MPA contrasts both with the situation that existed historically in the archipelago, where there was exploitation of breeding green turtles and their eggs (Sheppard et al. 2012), and with the conservation threats that sea turtles currently face elsewhere. For example, in some parts of the world sea turtles are still

captured, legally and illegally, for human consumption (e.g., Campbell & Lagueux 2005). Green turtles may also be subject to mortality through fishery bycatch and through boat strikes (e.g., Fiedler et al. 2012; Denkinger et al. 2013). The remoteness of the Chagos Islands from the nearest human settlement and presence of fisheries patrols means that human activity, including illegal fishing, may be limited, although assessing the extent of illegal activity remains an important management issue for the Chagos MPA (Sheppard et al. 2012) and for large MPAs in general (Pala 2013a).

Some transmitter-equipped individuals quickly started their post-breeding migration while others remained at Diego Garcia for several weeks. This difference between individuals likely reflects where each individual was in their sequence of clutches at the time the satellite tag was attached; by chance some individuals were equipped after they laid their final clutch for the season, while others were equipped earlier in their clutch sequence. Sea turtles may lay several clutches of eggs during a single breeding season. The typical internesting interval is around 15 days (e.g., Hays et al. 2000). Our results support the suggestion that satellite tagging may be used to assess the clutch frequency of individuals and hence be used in population monitoring (Weber et al. 2013).

It is not surprising that green turtles tracked from the Diego Garcia nesting beaches traveled to shallow foraging sites and remained at these sites for an extended period because green turtles, and other hard-shelled species, often maintain fidelity as adults to distinct foraging sites (Broderick et al. 2007). Furthermore, for green turtles these foraging grounds tend to be in shallow water because adults are herbivores feeding on seagrass and macro-algae, which are maximally abundant in shallow euphotic water (Broderick et al. 2007; Ballorain et al. 2013). Individuals would most likely remain at these sites until they traveled back to the Chagos Archipelago to breed. What is surprising, however, is the distance of some of these migrations, given that surveys show that seagrass beds exist in the Chagos

Archipelago (Spalding 2005; C. Sheppard, personal communication) and in territories en route between Chagos and Somalia. Yet only 1 of 8 tracked individuals foraged within the Chagos Archipelago, and the 2 turtles that traveled to mainland Africa broke the record for the longest post-nesting migration published for a hard-shelled turtle (Hays & Scott 2013). At some sites where forage is available locally, green turtles do not tend to migrate long distances away from their breeding beaches (e.g. Cocos Keeling Islands Indian Ocean [Whiting et al. 2008]). However, this pattern is variable with, for example, some green turtles nesting in Cyprus traveling long distances to the North African Coast (Broderick et al. 2007), despite extensive seagrass beds close to their breeding beaches (Hays et al. 2002).

The location of foraging sites used by adult sea turtles may be determined opportunistically by the pattern of drift of those individuals while they were small juveniles being carried by ocean currents (Hays et al. 2010*b*). The broad dispersion of post-nesting females from the breeding beaches on Diego Garcia therefore point to variable ocean currents and hence a pattern of juveniles drifting in various directions from the island. This conclusion is supported by empirical observations from satellite-tracked drifting buoys that show very variable ocean currents in this part of the Indian Ocean (Shenoi et al. 1999). It is therefore probable that additional shallow coastal sites across the Indian Ocean might be used by other adult green turtles that breed at Chagos, highlighting the need to track more adults to characterize foraging habitat extent. Genetic studies examining connections between Chagos and other Indian Ocean reef sites demonstrate a predominant affinity to the western Indian Ocean for species such as the crown-of-thorn starfish (*Acanthaster planci*), 24 reef fishes, and the hawksbill turtle (*Eretmochelys imbricata*) (Sheppard et al. 2012). This pattern accords with the results of our study.

Our life history model for time spent in breeding versus foraging areas was relatively insensitive to the exact model parameterisation; this means our conclusions that most

individuals spend the majority of their time outside the MPA also likely applies to male turtles that may return more frequently to breed but also spend less time on the breeding grounds during each breeding season (Hays et al. 2010a). So in addition to the conservation utility of the Chagos MPA, our results highlight how targeted protection of small coastal foraging areas could supplement this large MPA and increase the amount of time migratory species are in protected zones. This conclusion of the value for networks of protected areas reiterates the need for international cooperation to protect migratory species, including sea turtles (e.g. Blumenthal et al. 2006, Schofield et al. 2013b, Scott et al. 2012) and has driven international conventions and ensuing regional agreements to help protect migratory species (e.g. Doukakis et al. 2009). Our findings show that these broad conclusions apply even to one of the world's largest MPAs. Our tracking results showed that, in some cases, the areal extent of foraging grounds was relatively small compared with the existing MPA and could be designated with a simple bathymetric contour, which might aid implementation, as has been suggested elsewhere (Schofield et al. 2013a).

International co-operation is needed to help the conservation of wide-ranging species, which highlights the value of the Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats in the Indian Ocean and South-East Asia (IOSEA Marine Turtle MoU). The signatory states have recently resolved to establish a network of sites of importance for marine turtles in the IOSEA region. These sites are expected to include nesting beaches, foraging grounds, and migratory corridors. In the Seychelles plans to establish a network of protected areas in the outer islands are underway. But, in most cases the protected areas will extend 1-2 km from the coast and are unlikely to encompass substantial amounts of adult foraging habitat, although they could provide effective protection to breeding habitat.

As with the Chagos MPA, a key issue associated with the IOSEA Marine Turtle MoU will be the effective implementation of conservation within any protected zones and prevention of illegal fishing and other activities that may negatively impact turtles. Otherwise to designate an MPA without effective means to protect it might inadvertently turn it into a target for poachers. In short, our tracking results suggest that the Chagos MPA and IOSEA Marine Turtle MoU might provide a holistic avenue for broad sea turtle conservation within the Indian Ocean.

Elsewhere in the world the combined protection of turtle breeding and foraging sites has been achieved. For example, in the Atlantic Ocean adult green turtles migrate from breeding areas at Ascension Island in the middle of the Atlantic to foraging grounds along the Brazilian coast (Luschi et al. 1997). So protection of the breeding beaches at Ascension Island, along with protection of green turtles on the coast of Brazil, encompasses the majority of their adult lives and underpins long-term increases in the size of the breeding population following targeted harvesting of individuals in the 19th and early 20th centuries (Broderick et al. 2006). Knowledge of smaller scale migrations and habitats of green turtles in the Dutch Caribbean have also bolstered their protection by small, coastal MPAs at both breeding and nesting grounds such as St Eustatius, St Maarten, Curaçao, and Bonaire (Debrot et al. 2005; van Buurt 2011). In some cases, as in the example of turtles in Brazil, effective conservation of endangered marine species can be achieved without the need for MPAs but through some other level of protection. For example, restrictions on the exploitation (e.g. harvesting) of sea turtles, which applies at many national levels, can be a key conservation measure even in areas where other types of fishing and marine harvesting are allowed (Stringell et al. 2013).

Our conclusion that even the largest MPAs should be supplemented by targeted smaller MPAs or national legislation and international agreements is likely to apply to a broad range of marine migrants spanning several taxa. Many marine mammals, fish, turtles

and birds are known to undertake long distance movements (Hein et al. 2011; Hays & Scott 2013), even though they generally have not been tracked directly in relation to large MPAs. But, established procedures now exist for tracking a variety of marine vertebrates, including the use of archival and pop-off tags for fish that do not surface (Ropert-Coudert & Wilson 2005). So tracking data sets are attainable for many migratory species, including tuna. In this regard, the value of the Chagos MPA has been debated for tuna which are commercially exploited within the Indian Ocean and may undertake large migrations (Pala 2013*a,b*). As with green turtles traveling to and from the Chagos MPA, a key challenge will be to use tracking data sets effectively to implement conservation planning that has a real impact.

Our results highlight the conservation value of any MPA that can effectively minimise poaching and harvesting at crucial reproductive stages, regardless of political challenges or challenges from the fisheries lobby or other sources. Whatever the fate of the MPA that encompasses the Chagos archipelago, the need for strict conservation at turtle breeding grounds remains clear.

Acknowledgments

G.C.H., J.A.M., and N.E. conceived project on which this paper is based and took part in the fieldwork; G.C.H. led the analyses and interpretation of the data; D.I. conducted the GIS analysis; G.C.H. led the writing, but all authors contributed to the writing. We are grateful for logistical support provided by BF BIOT, MRAG Ltd, NAVFACFE PWD DG Environmental Department, and many volunteers on Diego Garcia in October 2012. Funding was provided by a Darwin Initiative Challenge Fund grant (EIDCF008), the Department of the Environment Food and Rural Affairs (DEFRA), the Foreign and Commonwealth Office (FCO), College of Science of Swansea University, and the BIOT Scientific Advisory Group (SAG) of the FCO.

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Table 1. Details of the migration distance and destinations of green turtles tracked by satellite from the Chagos

Turtle identification number	Date satellite tag attached	Foraging location, days of data, number of locations	Oceanic crossing distance (km), duration (days), number of locations	Straightness index during oceanic crossing	Total migration distance (km), duration (days), number of locations
4394	18 Oct. 2012	Seychelles, 65, 275	2554, 40.4, 330	0.81	2554, 40.4, 330
61811	13 Oct. 2012	Somalia, 222, 1306	3741, 60.9, 1559	0.82	3741, 60.9, 1559
61813	13 Oct. 2012	Somalia, 91, 176	3230, 45.0, 949	0.93	3230, 45.0, 949
21914	17 Oct. 2012	Seychelles, 152, 784	3886, 57.6, 782	0.55	3886, 57.6, 782
21923	20 Oct. 2012	Seychelles, 72, 104	2828, 54.9, 106	0.76	2828, 54.9, 106
117568	23 Oct. 2012	Chagos Bank, 263, 874	166, 3.6, 16	0.43	166, 3.6, 16
117569	24 Oct. 2012	Seychelles, 208, 749	2517, 47.0, 239	0.84	2517, 47.0, 239
117570	24 Oct. 2012	Maldives, 133, 146	1314, 26.5, 54	0.77	1314, 26.5, 54

*The number of locations obtained during migration and while on the foraging grounds is detailed to illustrate migration routes and space use on the foraging grounds was well characterized. Foraging locations were not detailed, so 2-9 months of foraging location data were analyzed for each individual.

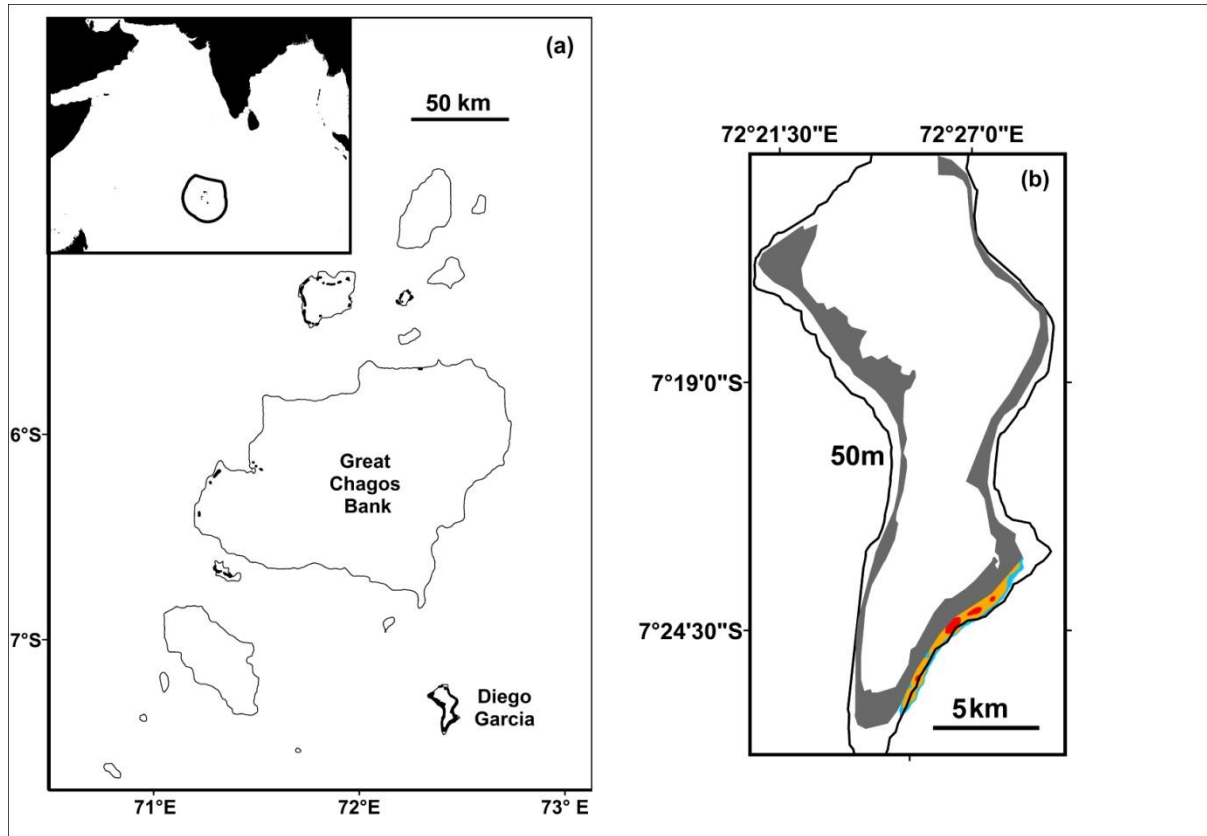


Figure 1. (a) Location of Chagos Archipelago MPA in the Indian Ocean (inset) and the island of Diego Garcia within the archipelago (black, land; solid line, 50-m depth contour that identifies the Great Chagos Bank). (b) Results of kernel density analyses for 8 green turtles at Diego Garcia prior to their departure on their postbreeding migration. The 50%, 90%, and 95% kernel home-range use areas are shown (red, orange, and blue, respectively). This kernel analysis is based on 3098 Fastloc-GPS locations.

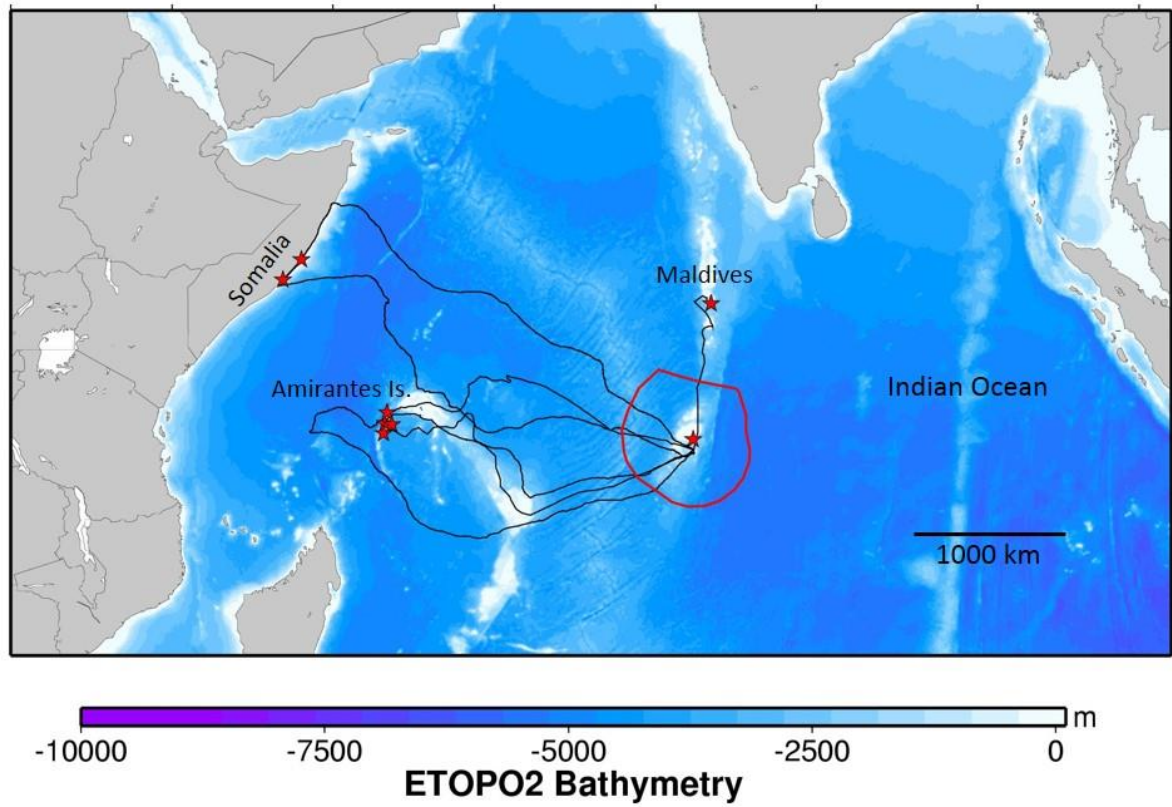


Figure 2. Movements of 8 adult female green turtles from their nesting beach on Diego Garcia (red stars, foraging ground location for each turtle; solid red line, extent of the Chagos Marine Protected Area). Four turtles traveled west to the Seychelles (Amirantes Island).

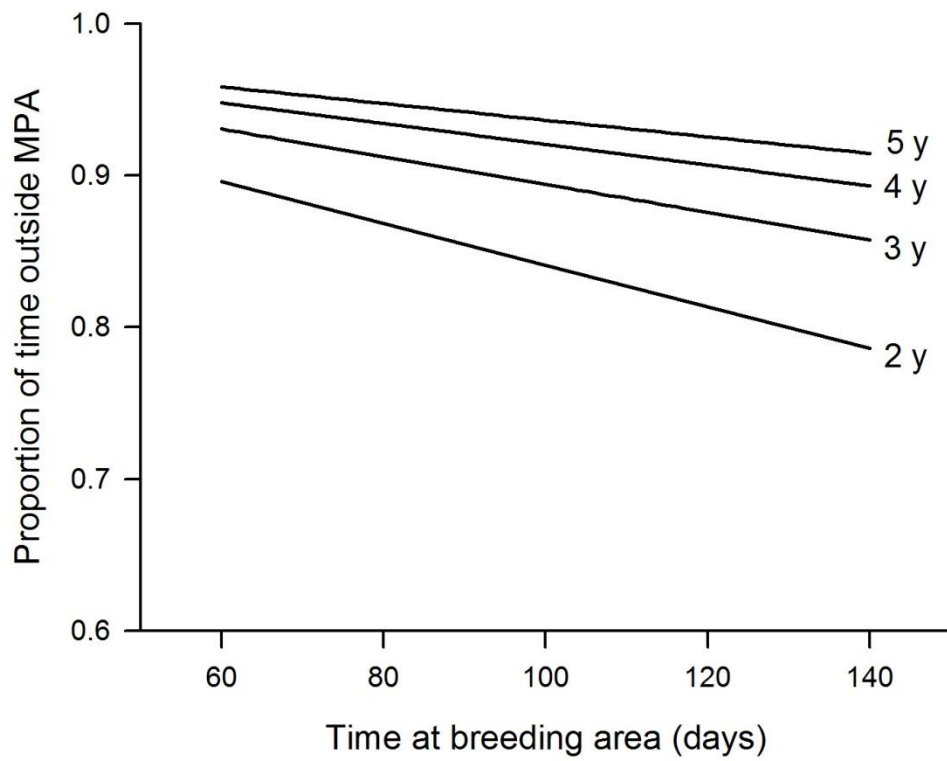


Figure 3. For turtles migrating to foraging grounds beyond the limit of Chagos Marine Protected Area (MPA), the proportion of their adult lives they would spend outside the MPA assuming different lengths of residence at the breeding ground in each breeding season (x-axis) and different intervals between breeding (lines).

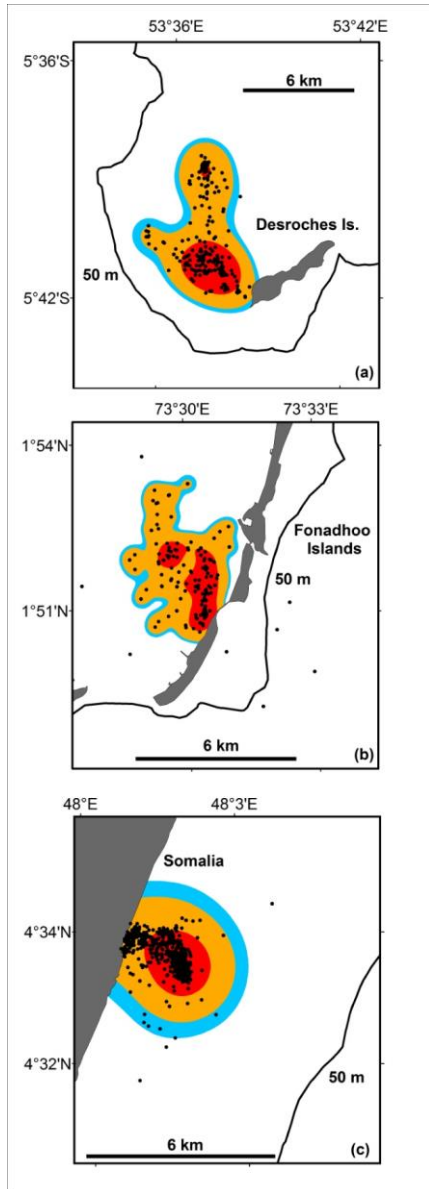


Figure 4. Fastloc GPS locations (dots) and results of kernel density analyses (colored areas) for 3 green turtles on their foraging grounds: (a) Desroches Island (Amirantes, Seychelles), (b) Fonadhoo Island (Maldives), and (c) coast of Somalia (red, 50% kernel home-range use; orange, 90% kernel home-range use; blue, 95% kernel home-range use areas shown; solid line, 50-m bathymetric contour; grey, land). Three examples are shown but all tracked turtles had the same general pattern of residence in shallow coastal areas.

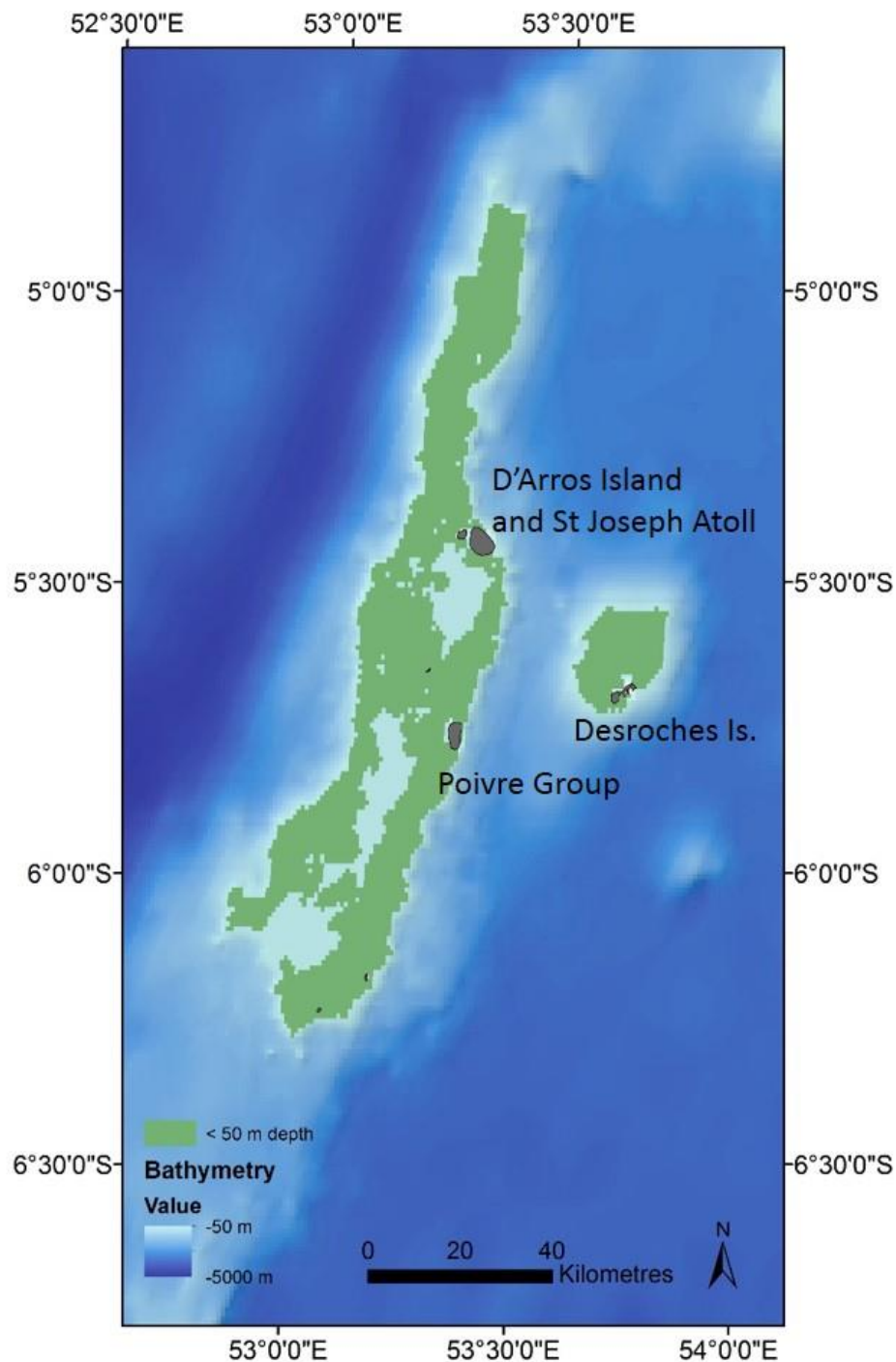


Figure 5. Space use (grey) by 4 green turtles tracked from Diego Garcia to their foraging grounds near the Amirantes Islands (Seychelles). See Fig. 2 for positioning of the Amirantes Islands in the Indian Ocean. The map shows the geographic extent of water <50 m deep (shaded green) to approximate potential foraging areas for green turtles. The main islands in the Amirantes group are identified.